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Zooplankton in relation to cyanobacteria across a geographic gradient in Archipelago Sea, northern Baltic

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Toxic cyanobacterial blooms are known to be a growing problem in many types of water bodies. Cyanobacteria are also known to affect zooplankton community structure. In this study, we assessed the possible impact of cyanobacterial blooms on zooplankton species composition. Altogether 20 locations on a geographical gradient were sampled in the Archipelago Sea in the northern Baltic during late summer 2003. We analyzed the data using multivariate methods and linear regression. The Mantel test of matrix correspondence revealed a statistically significant relationship between zooplankton species composition and cyanobacterial composition in July. The regression analysis showed a strong negative relationship between the cyanobacterial and copepod abundances. No relationship was found between cladocerans and cyanobacteria. A clear positive relationship was observed between rotifers and cyanobacteria. In conclusion, negative interactions may occur between certain zooplankton taxa and cyanobacteria in the Archipelago Sea, at least in midsummer. These interactions seemed to be associated with geographic zones within the archipelago.

Introduction

Toxic cyanobacterial blooms are known to be a growing problem in fresh and marine water bodies in several parts of the world. Toxic products of cyanobacteria have been causing human, livestock, wildlife and fish poisoning. Toxins of cyanobacteria are also known to affect profoundly both zooplankton community structure (Hietala *et al.* 1995, Christoffersen 1996, Agraval *et al.* 2001) and secondary production (Gulati 1990, Christoffersen 1996, Agraval *et al.* 2001).

The Baltic Sea suffers from periodic cyanobacterial blooms. The study of Sellner *et al.* (1994) indicated the growth rates of the two copepods (*Eurytemora affinis* and *Acartia bifilosa*), feeding on cyanobacteria, being substantially lower than copepods feeding on similar levels of good quality nutrition. Toxic cyanobacteria significantly reduced egg production in *Eurytemora* and *Acartia*. However, Reinikainen *et al.* (2002) found cyanobacterial toxins not to affect copepod egg survival.

Copepods are not the only animals affected by cyanobacteria. In their study of the water flea *Daphnia pulex*, Hietala *et al.* (1995) found that the most important life-history characters such as lifetime, clutch size, age and size at first

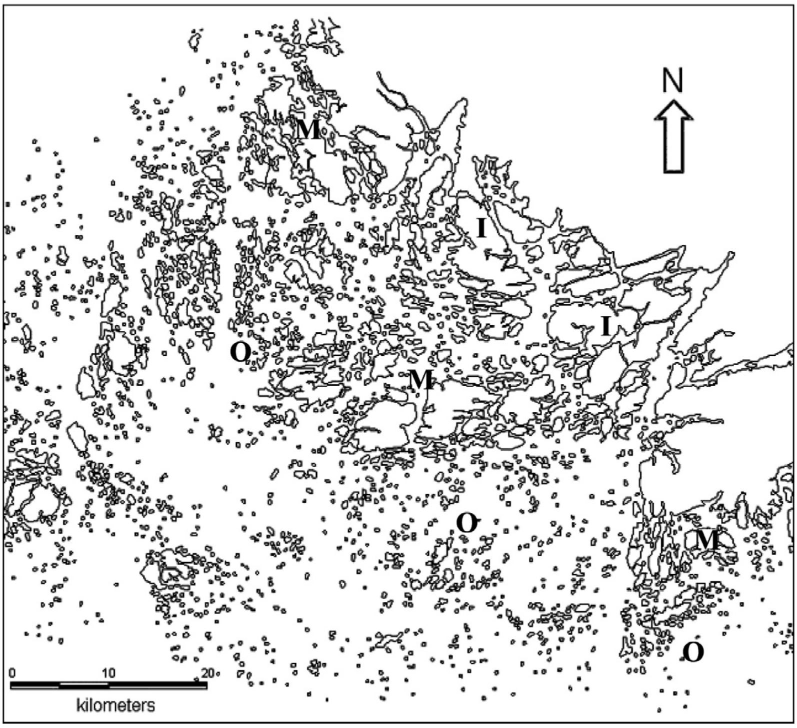

Fig. 1. The study area in the AS indicating the division into the outer (O), mid (M) and inner (I) archipelago. The area is located on the south-east coast of Finland (60°N, 22°E).

reproduction are all negatively affected by the presence of cyanobacteria. These results indicate that recruitment could show bloom-induced shifts in zooplankton species composition.

However, little is known about the temporal and spatial differences in the interactions between cyanobacteria and zooplankton. In our study two macroecologic factors affecting the composition of the zooplankton community were examined in the Archipelago Sea, northern Baltic. The aim was to assess whether there is an interaction between cyanobacteria and zooplankton species composition, and if there are any differences in the possible interactions in space and time.

We set geographical location as a null hypothesis explaining the variation in zooplankton species composition. Cyanobacterial species composition and hydrographic factors were set as alternative hypotheses.

Material and methods

Study area

The Archipelago Sea (AS) (Fig. 1) is divided into the outer- mid-, and inner zones (Jaatinen 1960). The inner archipelago is characterised by having more land than water. The percentage of land decreases as one moves from the interior archipelago to the outer archipelago, where there is already a greater proportion of water area than land area. Therefore, the physical factors (e.g. temperature, salinity, turbulence, etc.) vary between the zones. The zooplankton community may also differ in structure in geographically distinct locations. There is some evidence for this on a larger-scale in the Gulf of Finland and northern Baltic Sea (Viitasalo *et al.* 1990, 1995, Viitasalo 1992, Flinkman *et al.* 1991).

Collecting the data

Altogether 57 zooplankton samples were collected from 20 locations (Fig. 2) in the outer-, mid-, and interior northern Baltic archipelago on 14 July, 2 August, and 3 September 2003. The samples were gathered from depths 25–0 meters using a 100 mm net and were stored in 250 ml bottles. Five millilitres of formalin was added to preserve the zooplankton.

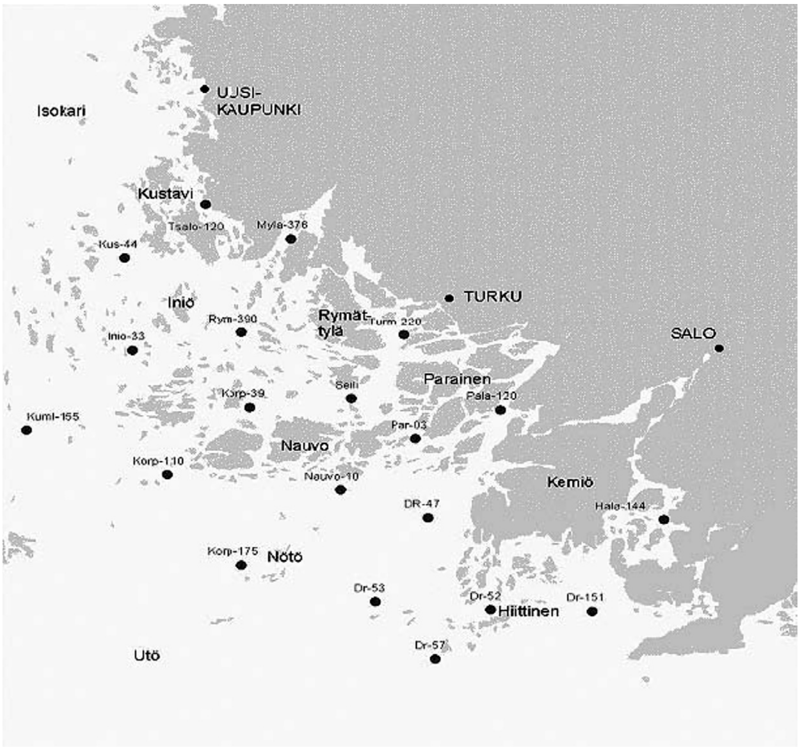

Fig. 2. The sample collection points in the AS. Other notations as in Fig. 1.

The following chemical and physical attributes of seawater were recorded at the sampling sites: ammonia, nitrate, phosphate, chlorophyll *a*, total phosphorus and total nitrogen concentrations, temperature and conductivity.

We analyzed the obtained samples with an Utermöhl reverse microscope using 5- and 10-ml cuvettes. Dense samples (having large quantities of animals and/or cyanobacteria) were diluted in order to make counting easier. All zooplankton species were counted. Individuals were mainly identified to genus level. With copepods, the nauplius, copepodite and adult stages were counted separately. The abundances counted in samples were extended to individuals per litre.

The cyanobacteria samples were collected and analyzed by a different group (J. Forsman, J. Ulenius, H. Seiko, E. Kosonen and J. Suomela unpubl. data). The samples were collected from the same sites as our plankton samples. The samples were analyzed using the same methods as we did. Cyanobacterial quantities were counted as the amount of 100 mm long filaments in subsamples, up to 200 filaments. Values of filaments per litre were used in the analysis.

Data analyses

Each month of the data was analyzed separately because plankton organisms have a clear temporal distribution pattern. We constructed three sites × species matrices, from the sampled zooplankton data, with 24 columns (species) and 19 rows (sites) each. These matrixes were used to calculate Bray and Curtis dissimilarity matrixes. This distance measure is particularly suitable for quantitative data (Legendre and Legendre 1998). This was done in order to model the resemblance between the sample sites by the means of community composition.

We also constructed two additional sets of data matrixes, for cyanobacteria and water chemistry. The same resemblance measure that was used for zooplankton was also applied for the cyanobacteria data (19 sites and 3 species for each matrix). An Euclidian distance coefficient was calculated for the geographical coordinates of the sample sites. The same coefficient was also used for the data considering water chemistry (each matrix having 19 sites and 8 descriptors). Euclidean distance is suitable for data,

Table 1. A list of identified taxa (including different life stages of copepods) within the archipelagic zones in different months. The letters m, f, c, and n after the copepod genus names stand for male, female, copodite, and nauplius, respectively. The values represent total abundances (indiv. per m^3), and are thus only interpretable as a relative measure of abundance.

	Archipelagic zone									
	Inner			Middle			Outer			Total
	July	August	September	July	August	September	July	August	September	
Rotifera:										
Keratella quadrata	1149919	317398	366829	286341	399512	280325	4070569	971545	285203	8127642
Synchaeta	143902	43902	35122	306667	118569	257073	2952520	421057	510000	4788813
Keratella cochlearis	62846	112927	71057	84715	241789	30732	85203	110244	177561	977073
Kellicottia longispina	0	0	0	0	0	0	0	813	0	813
Cladocera:										
Podon	67886	0	7317	80976	3577	3252	161626	5366	10081	340081
Bosmina	15691	10732	54472	3089	6179	4390	22114	5610	1463	123740
Pleopsis	0	0	0	0	0	3902	79675	81	0	83659
Daphnia	0	5691	21951	0	16423	10569	0	0	0	54634
Evadne nordmanni	12195	0	0	5691	0	1626	24715	488	976	45691
Cercopagis pengoii	0	81	0	0	813	0	0	569	976	2439
Sida crystallina	0	0	813	0	325	0	0	0	0	1138
Copepoda:										
Acartia n	32683	172846	48374	244390	164715	173659	47154	237317	341545	1462683
Acartia f	21870	35772	350813	15610	66016	146179	13984	101382	93659	845285
Acartia c	236341	49837	106423	26179	69268	37886	33171	183984	79106	822195
Eurytemora n	60488	33008	20163	59837	72846	74146	39024	66016	141382	566911
Eurytemora c	110000	26423	2439	23577	55935	32033	24390	24715	35610	335122
Temora c	111870	3902	4228	7805	38374	0	1301	111301	4228	283008
Acartia m	1301	27236	52114	4065	25041	27154	7154	31789	7073	182927
Eurytemora f	20813	8211	11382	9106	7642	28293	12358	16992	7236	122033
Temora n	1463	81	4878	2764	2276	0	9106	18211	49837	88618
Temora f	6585	244	0	650	11382	0	650	56911	3577	80000
Limnocalanus c	14146	8374	0	0	13659	0	0	34146	2276	72602
Eurytemora m	3252	5528	1626	5203	4228	17236	5528	5203	2683	50488
Limnocalanus f	976	650	0	0	325	0	1951	26829	0	30732
Limnocalanus n	0	0	0	0	0	0	0	27073	569	27642
Centropages c	650	488	17886	325	1301	325	650	407	61	22093
Centropages f	1301	0	6504	5041	0	1301	2602	650	0	17398
Cyclopoida c	0	2276	0	650	4228	0	8130	1626	61	16972

Pseudocalanus n	0	569	0	0	2276	0	650	6748	3902	14146
Pseudocalanus f	976	81	0	0	325	2602	650	650	0	5285
Temora m	0	0	0	163	4878	0	0	0	0	5041
Pseudocalanus c	0	0	0	0	0	0	650	3577	0	4228
Limnocalanus m	0	1301	0	0	0	0	0	1789	0	3089
Centropages n	0	0	1626	0	0	325	0	0	0	1951
Cyclopoida f	0	0	0	163	650	0	0	0	61	874
Centropages m	0	650	0	0	0	0	0	0	61	711
Cyclopoida n	0	0	0	0	0	0	0	488	0	488
Pseudocalanus m	0	0	0	0	0	0	0	0	0	0
Cyclopoida m	0	0	0	0	0	0	0	0	0	0
Others:										
Balanus	44390	7480	5691	38211	2602	7317	56260	3659	4878	170488
Gastropoda	2683	1301	0	3415	2276	488	51382	43496	1463	106504
Bivalvia	6667	650	0	22114	1951	0	26341	2033	976	60732
Polychaeta	976	12276	5203	325	6179	3740	1626	9593	2520	42439
Gammarus	0	0	0	0	650	0	0	81	0	732

where zero values are not treated the same way as other values (as with species absence).

We applied the Mantel test to see if there was a correlation between the different distance matrixes (Legendre and Legendre 1998). In a simple Mantel test two matrixes are compared. First a Pearson correlation is calculated between the matrixes and after this, the other matrix is shuffled several times (a default procedure shuffles the matrix 999 times) and the correlation is recalculated each time. This is done in order to construct a distribution of correlation coefficients. The original coefficient is then compared with this distribution in order to determine its statistical significance. The Mantel statistics were calculated for pairs formed by zooplankton matrix and cyanobacteria matrix, zooplankton matrix and water chemistry matrix and zooplankton matrix and geographical distance matrix. These tests provided a global significance for the relationships between the analyzed datasets.

As a result of these analyses we selected the data containing zooplankton and cyanobacterial numbers in July for further analysis. First a simple rank correlation test was conducted to rule out non-related pairs of variables. As a result, we selected the most abundant zooplankters along with the two most abundant cyanobacteria. Among the zooplankton species we chose the adults and nauplii of *Acartia* and *Eurytemora* of the copepods and *Synchaeta* and *Keratella* of the rotifers. Also the combined numbers of the three functional groups of zooplankton (copepods, cladocerans and rotifers) were selected. *Aphanizomenon* and *Anabaena* were chosen of the cyanobacteria. All selected variables were transformed using a natural logarithm in order to make them distribute more normally. The relationships between these selected zooplankton taxa and cyanobacteria were tested with simple regression analyses.

The JMP 3.2.1 (SAS systems) statistical software and Le Progiciel R 4.0 multivariate software (Legendre and Vaudor 1991) were used in the analysis.

Results

In all, we found 24 species of copepods, rotifers, cladocerans and other sea invertebrates in the samples (Table 1). The sampled species differed greatly in abundance, rotifers being most abundant and cladocerans least abundant of the biggest groups of zooplankton. We also observed significant variation in zooplankton numbers between different sample sites and different sampling months.

The Mantel test revealed a positive correlation between the distance matrixes of zooplankton species and cyanobacteria in July and zooplankton species and geographical distance in August. We observed no correlation between these matrixes in September. There was also no globally significant correlation between the distance matrixes of zooplankton and water chemistry during any of the analyzed months (Table 2; means and standard deviations in different months for the cyanobacteria taxa are given in Table 3, and for the hydrographic variables in Table 4).

We applied one-way ANOVA to find out if the observed geographical segregation in August was caused by one or several hydrographic fac-

Table 2. Statistical details for the Mantel test between zooplankton community composition and three other datasets in three summer months. *r* refers to Pearson correlation coefficient. Statistical significance was estimated using 999 permutations.

Month	Explanatory dataset	Mantel statistics	
		r	*p*
July	cyanobacteria	0.192	0.035
	geodistance	0.155	0.069
	water chemistry	0.099	ns
August	cyanobacteria	0.052	ns
	geodistance	0.379	0.001
	water chemistry	0.095	ns
September	cyanobacteria	0.172	0.064
	geodistance	0.047	ns
	water chemistry	0.212	ns

Table 3. Mean biomass (mg l^{-1}) and standard deviation for three cyanobacteria genera during three summer months in the inner, middle, and outer zone of the Northern Baltic Sea archipelago.

Zone	Month	*Aphanizomenon*		*Anabaena*		*Nodularia*	
		Mean	S.D.	Mean	S.D.	Mean	S.D.
Inner	July	28045.8	49057.7	26438.3	58095.2		
	August	264247.0	376458.4	7390.9	4453.4	373.5	315.9
	September	116250.7	206324.2	2161.1	3941.0	364.9	774.6
Middle	July	15613.7	14431.0	11386.9	12494.5		
	August	76513.4	43263.0	20100.8	16460.8	3509.4	2969.9
	September	29806.4	28865.2	1752.2	1140.5	530.2	810.3
Outer	July	306788.8	280918.6	126613.5	103305.4	893.7	1293.2
	August	36280.9	11883.7	16292.9	12672.4	2023.5	1926.9
	September	39870.0	15523.2	10480.4	11808.3	1324.6	1295.3

Table. 4. Mean and standard deviation values for the measured water chemistry variables in different months. n = 19 for all months.

	July		August		September	
	Mean	S.D.	Mean	S.D.	Mean	S.D.
NH^{4+} (µg l^{-1})	3.95	4.92	4.22	5.00	2.66	2.43
PO_4^{3-} (µg l^{-1})	3.21	2.50	1.92	1.57	3.16	2.48
Chlorophyll *a* (µg l^{-1})	0.04	0.17	1.06	1.52	0.00	0.00
Total P (µg l^{-1})	18.64	3.75	19.96	4.82	18.34	4.23
Total N (µg l^{-1})	321.32	38.62	357.11	52.71	314.74	24.97
Temperature (°C)	17.67	2.52	20.21	2.62	14.83	0.92
NO_2^- (µg l^{-1})	3.86	1.28	3.18	0.42	4.46	3.51
Conductivity (µS)	750.00	461.80	748.68	475.00	796.32	489.38

tors. These analyses revealed mean seawater ammonium concentration to be significantly greater in the inner zone (df = 2, SS = 161.66, $F = 4.48$, $p = 0.027$, $R^2 = 0.36$), as compared with that in the other zones. Moreover, during the whole study period, seawater phosphate concentration was significantly lowest in the outer zone (df = 2, SS = 41.21, $F = 4.51$, $p = 0.016$, $R^2 = 0.14$). The same applied also to ammonium concentration (df = 2, SS = 286.43, $F = 10.56$, $p = 0.0001$, $R^2 = 0.28$).

Although the Mantel correlation between geographic location and zooplankton community was not globally significant, individual groups did differ in abundance between the archipelagic zones (Table 5). On a logarithmic scale, copepods were least abundant in the outer zone. In contrast, rotifers were most abundant in the outer zone. *Acartia* adults had a similar pattern to that of all copepods and *Synchaeta* to that of all rotifers. Moreover, abundances of *Aphanizomenon* ($\chi^2 = 9.49$, df = 2, $p = 0.009$) and *Anabaena* ($\chi^2 = 7.89$, df = 2, $p = 0.019$) differed also between the zones. Both cyanobacteria were most abundant in the outer zone.

The regression analyses revealed a strong negative relationship between the cyanobacterial, especially *Aphanizomenon*, and copepod abundances (Fig. 3). More specifically, *Eurytemora* copepods seemed to have a clear response to increasing *Aphanizomenon* abundance. Abundances of *Acartia* adults had also a tendency to decrease with increasing *Aphanizomenon* abundance, but this relationship was not significant. Similarly there was a non-significant negative trend in the total copepod abundance in relation to *Anabaena*. Contrary to copepods, rotifer seemed to have a positive relationship with *Anabaena* (Fig. 4). Apparently both *Synchaeta* and *Keratella* increased with increasing abundance of *Anabaena*. Moreover, *Synchaeta* seemed also to increase in abundance in relation to increasing abundance of *Aphanizomenon*.

Discussion

The primary aim of our research was to examine if the variation in cyanobacterial abundances could explain the variation observed in zooplankton species composition over a geographical gradient. The Mantle test proved the cyanobacterial abundances to explain the variation in zooplankton abundances and distribution in July to some extent. Closer examination revealed a negative relationship between *Aphanizomenon* abundance and the abundance of *Eurytemora* copepods and combined copepod numbers on a logarithmic scale. Sellner *et al.* (1996) found *Acartia* and *Eurytemora* to have a reduced growth rate when grown in a solution with cyanobacterial toxins. Moreover, they found the fecundity of the copepods to be reduced. Our results showed a decline in *Eurytemora* nauplii, which could indicate a decrease in fecundity due to cyanobacteria.

There is no record of toxic *Aphanizomenon* and *Anabaena* strains in the Baltic Sea. On the contrary, there is evidence of cyanobacteria being low quality food to copepods because of their protease inhibitors (Agraval *et al.* 2001). Cyanobacteria are known to increase in abundance on the expense of phytoplankton leaving little or no choice of nutrition for zooplankton. The fact that we observed a significant relationship between zooplankton and cyanobacteria only in July could be due to the very large cyanobacteric blooms in July (e.g. Kiirikki *et al.* 2001). Cyanobacterial abundances decreased from the middle of July to the beginning of August. Thus it is reasonable to consider that cyanobacterial abundances are high enough only in July to suppress zooplankton.

A positive relationship was observed between rotifers (mainly *Synchaeta* spp. and *Keratella* spp.) and *Anabaena* on a logarithmic scale. *Syn-*

Table 5. Statistical details for one-way ANOVA between the archipelagic zones and various zooplankton groups in July. $n = 19$, df = 2.

Group	SS	F	R^2	p
Copepods	10.73	5.71	0.42	0.014
Cladocerans	0.83	0.40	0.07	0.68
Rotifers	11.92	5.11	0.41	0.02
Acartia adults	12.23	3.54	0.32	0.055
Eurytemora adults	5.27	2.55	0.25	0.11
Acartia nauplii	4.14	1.54	0.18	0.25
Eurytemora nauplii	3.52	2.27	0.23	0.14
Synchaeta	32.77	9.62	0.56	0.002
Keratella	10.86	3.31	0.31	0.065

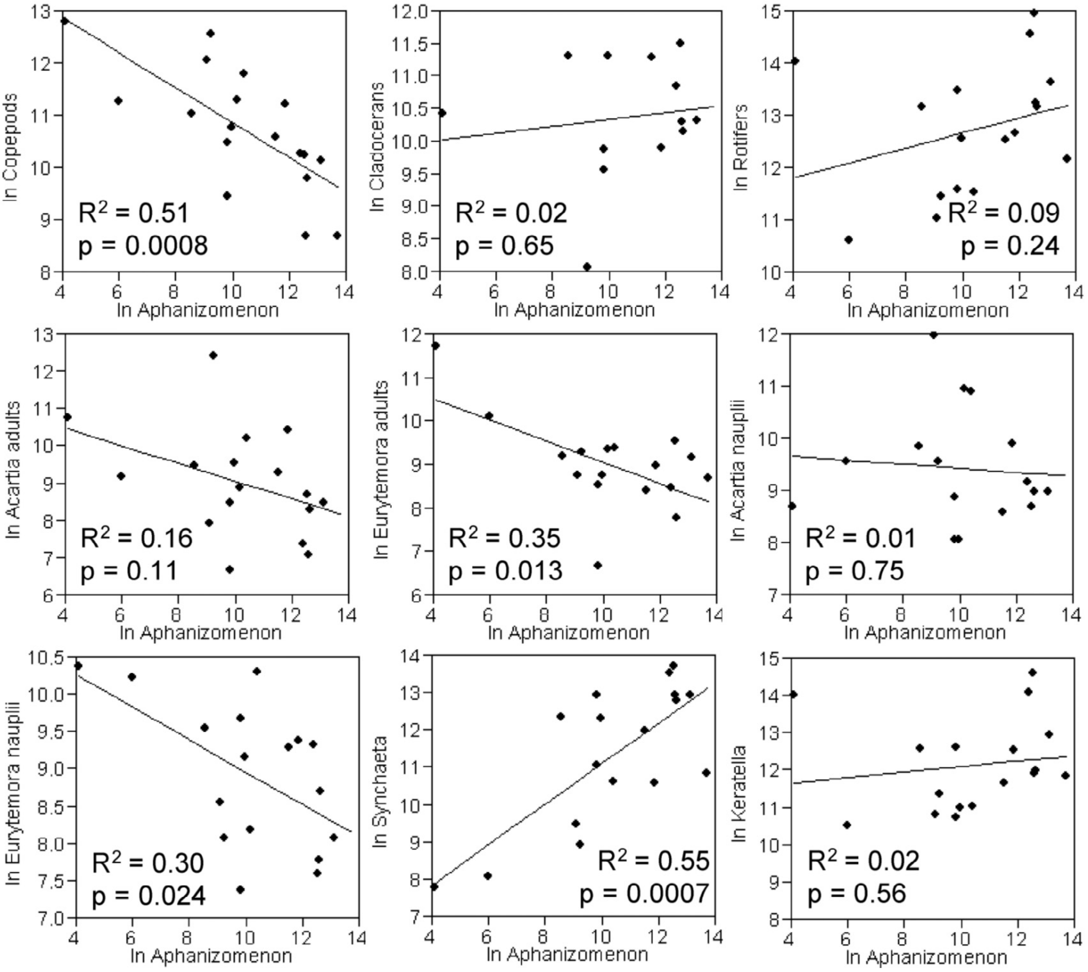

Fig. 3. The abundances (individuals per litre) of selected zooplankton groups plotted against the abundance (the amount of 100 mm long filaments per litre) of *Aphanizomenon*. The data points represent different locations in the study area in July 2003. The order of the data points is in no relation to geographical location.

chaeta rotifers were also positively related with increasing *Aphanizomenon* abundance. Gilbert (1990) reported a similar result. He found high densities of rotifers to be associated with cyanobacterial blooms. Many studies have reported cyanobacteria being low quality and even toxic food to copepods and cladocerans (e.g. Sellner *et al.* 1996, Gilbert 1990, Agraval *et al.* 2001). According to Gilbert (1990), cyanobacteria prevent the suppression of rotifers by large cladocerans and thus lead to the dominance of rotifers. Our data did not conform to these studies considering cladocerans. We observed no significant relationship between cyanobacterial and cladoceran abundances.

In the brackish waters of the AS the distribution of many species is considered to be related to geographical zones (Hänninen *et al.* 2000, Vahteri *et al.* 2000, Hänninen and Vuorinen 2001, Vuorinen *et al.* 2002, O'Brien *et al.* 2003). We observe a globally significant correlation between site location and zooplankton species composition, although this only took place in August. Further analysis indicated seawater ammonium concentration to be responsible for the observed pattern. In fact, various zooplankton groups did differ in their abundance between the archipelagic zones in July. For example, copepods were most abundant in the inner zone, and least abundant in the outer zone, rotifers

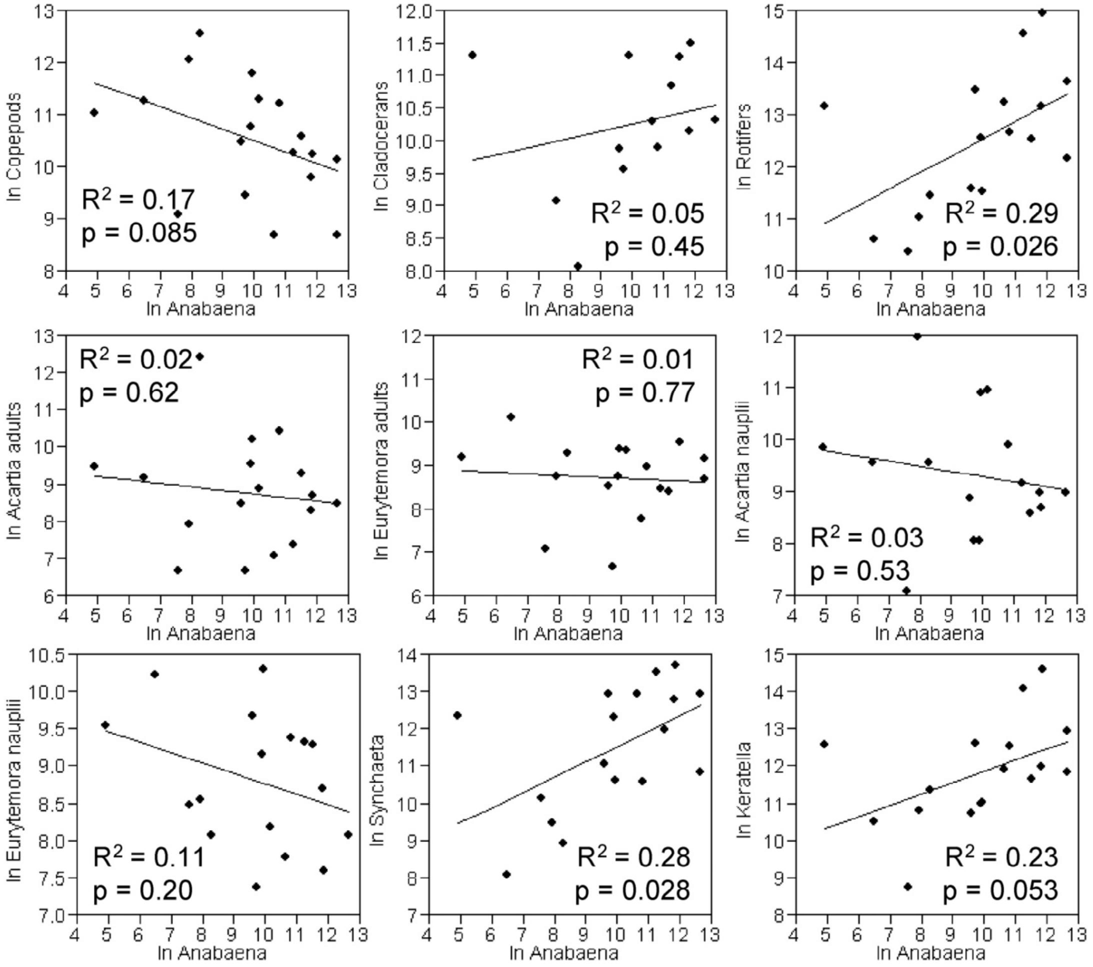

Fig. 4. The total abundances (individuals per litre) of selected zooplankton groups plotted against the abundance (the amount of 100 mm long filaments per litre) of *Anabaena*. Notation as in Fig. 3.

displaying an opposite pattern. Moreover, cyanobacteria were observed to be most abundant in the outer zone.

Seawater properties in the inner-, middle-, and outer zones remained relatively similar during the study period. However, the average seawater ammonium and phosphate concentrations were lower in the outer zone, as compared with those in the other zones. Blooms of nitrogen fixing cyanobacteria (e.g. *Aphanizomenon* and *Anabaena*) are controlled by phosphorus availability (Kononen *et al.* 1993). This does not however explain the fact that the greatest abundances of cyanobacteria were observed in the outer zone, where phosphate concentration was at its lowest. It is also possible that the cyanobacteria abundances were influenced by a favourable N:P ratio (Kononen *et al.* 1996). However, such a relationship was not evident in our data.

One reason for the zones being very similar in the means of hydrographic properties may be the fact that there has been no major seawater influx from the North Sea for thirty years, and thus the salinity in the Baltic Sea has remained uniform.

We conclude that negative interactions may occur between certain zooplankton taxa and cyanobacteria in the AS, at least in midsummer. These interactions seemed to be associated with geographic zones within the archipelago. Copepods were most abundant in the inner zone and rotifers in the outer zone, which was related to an increasing abundance of cyanobacteria from the inner- to the outer zone. Furthermore, this trend was possibly related to a difference in seawater ammonium and phosphate concentrations between the archipelagic zones.

We interpreted the negative interaction between copepods and cyanobacteria to have been caused by the low palatability and nutritional value of cyanobacterial filaments. Cyanobacteria may be more competitive in the low nitrogen conditions of the outer archipelagic zone, in relation to eucaryotic phytoplankton. This would leave copepods with little or no alternatives in their nutrition. As mentioned earlier, the increase in rotifer numbers could have been due to cyanobacterial toxins reducing the number of cladocerans, the rotifer predators. However, this seems unlikely, as these toxins have not been found in the Baltic Sea.

There appears to be considerable variation in zooplankton species abundances between the summer months in the Baltic Sea. Due to this temporality, we recommend studying this system for several years to find out whether there is variation between years and whether the observed situation is repeating itself. Moreover, the current hydrological conditions in the AS are very homogenous across a long geographical gradient. The salinity in the region and the whole Baltic Sea has not been lower in thirty years. If there is no salt influx to be expected from the North Sea, the species composition of the Baltic Sea could be expected to resemble inland waters even more.

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